OVIPOSITION BEHAVIOUR OF *CERATOSOLEN FUSCICEPS* MAYR (AGAONIDAE: HYMENOPTERA) AND THE MECHANISM OF POLLINATION IN *FICUS RACEMOSA* L.[1]

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(*With four text-figures*)

Ceratosolen fusciceps Mayr breeds in the gall ovaries of *Ficus racemosa* L. The *Ficus* species depends exclusively on the females of these insects for pollination. The female wasp enters the young syconium through its ostiole which is blocked with thickly packed bracts. The morphological adaptations of the female for this penetration and the different stages of oviposition are briefly discussed.

Prior to eclosion from the ripe figs, the female wasps actively load pollen grains into their paired mesothoracic pollen pockets. Inside the tender figs, they deliberately unload the pollen grains before the termination of each oviposition. The whole process of oviposition and pollen transfer in respect of one ovary takes about 50-70 seconds.

INTRODUCTION

Information on the oviposition and pollination behaviour of agaonids are scanty. Certain aspects of the oviposition behaviour of *Blastophaga psenes* that breeds in *Ficus carica* were observed by Grandi (1920 & 1929) and Joseph (1958), and of *Ceratosolen marchali* in *Ficus hispida* by Abdurahiman & Joseph (1976). The pollination behaviour of *Ceratosolen arabicus* and *Blastophaga quadraticeps*, the pollinators of *F. sycomorus* and *F. religiosa* respectively, were studied by Galil & Eisikowitch (1968a & b, 1969 & 1974) and Galil & Snitzer-Pasternak (1970). Galil *et al.* (1973) made a closer look on pollination in *F. costaricana* and *F. hemsleyana* by *Blastophaga estherae* and *B. tonduzi* respectively. Chopra & Kaur (1969) made a brief study on the pollination and fertilization in some *Ficus* species like *F. carica, F. racemosa, F. tsiela* and *F. virens*. Ramirez (1969) studied the mechanism of pollen transfer by some species of wasp genera including *Agaon, Allotriozoon, Blastophaga, Ceratosolen, Elisabethiella, Liporrhopalum* and *Pleistodontes*. Galil (1973), and Galil & Neeman (1977) studied in detail the pollen transfer and the mechanism of pollination in *F. fistulosa* by *C. hewitti*, and in *F. carica* by *B. psenes*. The present studies comprise a detailed analysis of the behaviour of oviposition and the mechanism and adaptations involved in pollination in the case of *Ceratosolen fusciceps* that breeds in the receptacles of *F. racemosa*.

MATERIALS AND METHODS

Ficus racemosa trees have a fair distribution in the Calicut University campus, where the present studies were undertaken. Ripe and tender figs of appropriate stages were collected from the trees. The females of *C. fusciceps* that eclose from ripe figs penetrate into the receptive tender figs provided. Such figs containing the females in the act of oviposition

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and pollination were observed under the Stereomicroscope with bright illumination. The pollen loading behaviour were studied in the ripe fig halves wrapped in transparent cellophane and observed under the microscope in the early morning. Anaesthetized adult females stained with alcoholic acid fuchsin (0.5% acid fuchsin in 70% alcohol) were utilized for the study of the "pollen pockets".

Observations and Results

The structure of the fig:

F. racemosa is monoecious with the male, female and 'gall flowers' occurring in the same syconium (Fig. 1). The male flowers are few in number and are arranged in 2-3 rows encircling the ostiole. The gall and female flowers are intermingled. The female 'seed flowers' have ovaries with long styles, while the 'gall flowers' have short styles and they are modified for the development of insects. The inflorescence is highly protogynous, the female flowers maturing first and the male flowers maturing only after 2-3 weeks. The stigmata of neighbouring gall and female flowers interconnect forming a 'syn-stigma'. Thus the syconial cavity is lined continuously, which prevents the slipping down of the polliinators between the styles and ovaries.

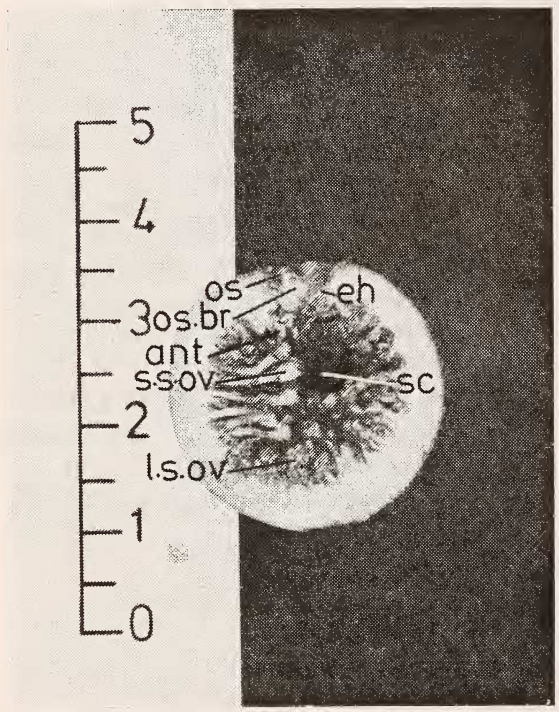

Fig. 1. Median longitudinal section of a ripe fig of *Ficus racemosa* L.

Abbreviations:

ant, anthers; eh, exit hole; l.s.ov, long-styled ovary; os, ostiole; os.br, ostiolar bracts; sc. syconial cavity; s.s.ov, short-styled ovary.

Oviposition

The eclosion of *Ceratosolen* females from mature figs occurs largely during the morning hours between 6 a.m. and 11 a.m. In the field, they fly in search of tender receptive figs for oviposition. Such figs of the female phase may be present either on the same tree or on other nearby trees. The *Ceratosolen* females wander over the surface of the tender figs till they locate the ostiolar opening by their antennae. Since the ostiole of the young syconium is thickly packed with overlapping bracts, the insect struggles hard to enter the syconium. It raises its abdomen and the head is pushed into the ostiole. The morphological adaptations of the insect such as the dorso-ventrally flattened head with serrated mandibular appendages and strongly built fore and hind legs, make its entry easy. The wings and flagella of the antennae are often lost during this strenuous effort of penetration. The time taken for the penetration varies depending on the age of the young figs, though, it is usually about 8-10 minutes.

After entry, the mutilated female moves on the surface of the stigmata for a few minutes

and then prepares for oviposition. The ovipositor which is kept horizontally ensheathed in the ovipositor sheaths is taken out by bending the abdomen and using her hind pair of legs. The hypopygium forming a triangular flap that encloses the ovipositor basally, is lowered and held vertical to the long axis of the abdomen. This organ supports and guides the ovipositor shaft during oviposition. The ovipositor sheaths and remains extended upwards from the tip of the abdomen. The site of penetration, namely, the stigmal opening is detected by the tip of the ovipositor which is provided with sensillae. The wasp rises on its legs and the tip of the ovipositor is moved back and forth on the stigmal surface. On locating the stigmal opening, the abdomen is raised and the ovipositor is introduced into the style of the gall ovary (Fig. 2). It is lowered slowly and the further bending of the abdomen brings about complete penetration of the ovipositor down the style and the egg is deposited in the ovule. The abdomen vibrates during oviposition and the wasp is found actively engaged in biting the stigmata with its mandibles. After the deposition of the egg, she withdraws her ovipositor. The ovipositor is not ensheathed and the wasp continues her egg laying in other 'gall ovaries'. The whole process of oviposition in a given ovary of *Ficus* takes about 50-70 seconds. After the oviposition, the female dies within the syconium.

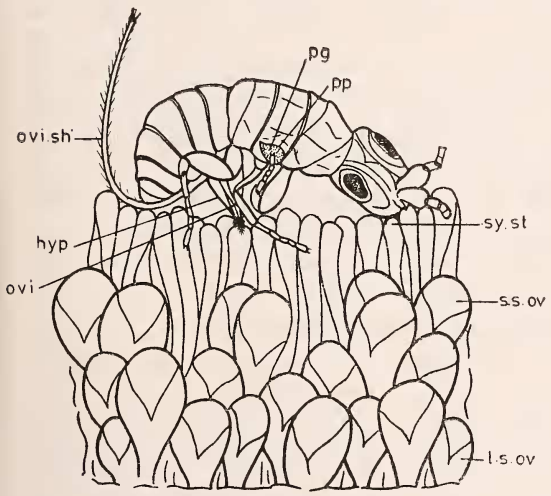

Fig. 2. Ovipositing female of *Ceratosolen fusciceps* Mayr at the pollination act.
hyp, hypopygium; l.s.ov, long-styled ovary; ovi, ovipositor; ovi.sh, ovipositor sheath; pg, pollen grains; pp, pollen pockets; s.s.ov, short-styled ovary; sy.st, synstigma.

Pollination

Prior to their eclosion from mature figs, the females of *C. fusciceps* actively load pollen grains in their specialised organs called 'pollen pockets'. These paired thoracic pockets are seen as triangular depressions on the ventrolateral sides of the mesothorax with their narrow ends directed backward (Fig. 3). Each

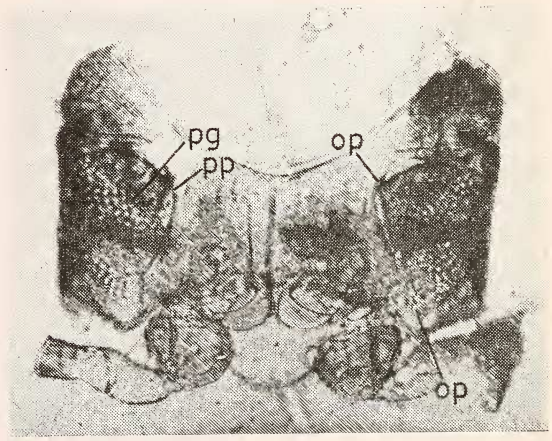

Fig. 3. Thoracic 'pollen pockets' with pollen grains. op, openings; pg, pollen grains; pp, pollen pockets.

pollen pocket (173 × 155 μ) bears two openings, one at the narrow inner end and the other at the anterior inner border.

The thoracic pockets are loaded with pollen grains in the early morning between 3 a.m.

and 6 a.m. After emergence from the galls, the female approaches the anthers previously cut down by males and pushes her head into its median slit. Keeping the anther sacs open by their antennal scapes, she crumbles the pollen grains within the anther and then performs the pollen lifting movements. The pollen grains are lifted from the anthers to the underside of the mesothorax by repeated swift alternating movements of the fore legs, dipping the arolia in the anther and raising them backward to the thorax. Then the wasp curves the thorax, and the pollen grains are brushed into the pockets by the sweeping movements of the fore coxae and their combs which are formed of a row of 16 stiff bristles on the inner margins of the coxae (Fig. 4). This

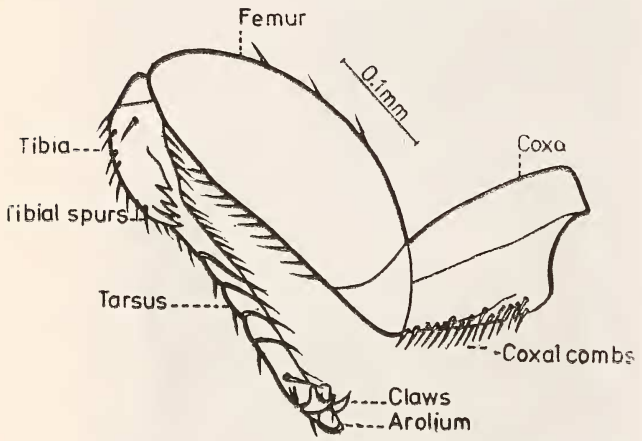

Fig. 4. Fore leg of *Ceratosolen fusciceps* Mayr showing 'coxal combs'.

shovelling movements are repeated several times after each sequence of pollen lifting movements. Such females escape out of the syconium through the exit holes gnawed by the males near the ostiole.

The unloading of pollen grains and the subsequent pollination of the *Ficus* inflorescence occur at the end of each oviposition in the young syconium. Before the termination of the oviposition, the female folds up her fore legs and scratches the pockets 3-5 times with her arolia and claws (Fig. 2). This simultaneous and alternating to and fro movements of the two fore legs shovel some of the pollen grains to the stigmata. Then she strikes the tarsi of the fore legs against each other and the arolia and claws are rubbed on the stigmal surface effecting the transference of pollen grains directly to the stigmata. These repeated pollination movements of the fore legs take about 3-5 seconds.

Discussion

Ceratosolen fusciceps deposit their eggs in between the nucellus and inner integument of the gall ovaries of *F. racemosa,* as shown in *B. psenes* of *F. carica* by Joseph (1958) and in *C. marchali* of *F. hispida* by Abdurahiman & Joseph (1976). The oviposition behaviour of all the agaonids studied are very similar. The hypopygium supports and guides the ovipositor during the process of egg laying. Unlike in the other agaonids the females of *B. quadraticeps* of *F. religiosa* remain stationary and exhibit no stigmal biting during oviposition (Galil & Snitzer-Pasternak 1970). *B. estherae* of *F. costaricana* (Galil *et al.* 1973) takes 3-4 minutes for the completion of oviposition, unlike *C. fusciceps* and *C. arabicus* which need only 50-70 seconds.

The pollination behaviour of *C. fusciceps* is akin to that of *C. hewitti* in the dioecious fig *F. fistulosa* (Galil 1973) and *C. arabicus* in *F. sycomorus* (Galil & Eisikowitch 1968, 1969 & 1974). The 'coxal corbiculae' as described by Ramirez (1969) is absent in *C. fusciceps.* The closed thoracic pockets with coxal combs are common features present in these pollinators. The pollination movements of *B. estherae* and *B. tonduzi* in *F. costaricana* and *F. hemsleyana* respectively (Galil *et al.* 1973)

are much more complicated by the presence of 'coxal corbiculae'. They use these corbiculae as shovels in addition to its role in the storage of pollen grains.

The pollination movements of *C. fusciceps* are deliberate, as in other pollinators, such as *B. quadraticeps, C. arabicus* and *C. hewitti.* The loading and unloading of pollen grains in the wasps are purposeful movements. Such a deliberate pollination movement is explained as 'Ethodynamic pollination' by Galil (1973b), in contrast to 'Topocentric pollination' in *F. carica. B. psenes,* the pollen vector of *F. carica,* lacks pollen pockets and they carry pollen grains in the 'inter-segmental concavities' of the body. The passive loading of pollen grains into these concavities occur when the body shrinks as a result of water loss following eclosion. In the young syconium, the body of the wasp swells due to the higher humidity and thus pollen grains indirectly come in contact with the stigmas effecting pollination (Galil & Neeman 1977).

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